

THE CAMPION RUSTS PUZZLE

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Two species of rust fungi, *Puccinia arenariae* and *P. behenis*, both of which grow on living leaves of red campion, *Silene dioica*, have been known to occur in Britain since the pioneer days of rust studies in the 19th and early 20th centuries (Wilson & Henderson, 1966 who considered them to be 'common' and 'scarce' respectively). When recording of rust fungi increased during the second half of the 20th century there was an abundance of records of *P. arenariae* on red campion with very few sporadic records of *P. behenis* at widely scattered locations. In Warwickshire, where detailed recording of fungi began in 1965, only *P. arenariae* was recorded until the first find of *P. behenis* in 2002. Was this an example of the sporadic occurrence of *P. behenis*? However both rust species continued to be recorded in most subsequent years and curiosity about the occurrence of *P. behenis* reached a peak in 2010 when the 1km grid squares of the eight earliest Warwickshire records of *P. arenariae* (1966-1976) were revisited. *P. arenariae* was re-found in six of these but *P. behenis* was present in a different combination of six. The 'scarce' rust appeared to be scarce no longer in Warwickshire and the puzzle was whether this was so elsewhere in Britain. It was time to establish the current status of the two species nationwide and in 2011 the opportunity arose to put an appeal for specimens of these rusts on the Field Mycology section of the British Mycological Society's website.

The 2011 Appeal

The two species in the survey

Although many rust fungi have complex life cycles with a specific sequence of up to five spore stages on two alternate host plants, these two rust species form only one or two spore stages and are readily distinguished microscopically. *P. arenariae* forms only two-celled teliospores which normally germinate immediately to form basidiospores on the telia (Figs. 1 & 2). Germination of teliospores formed in the autumn may be delayed until the following spring (Wilson

& Henderson, 1966). In Britain *P. behenis* forms almost entirely one-celled urediniospores, rarely forming two-celled teliospores (Fig. 3). Although pustules of the two species differ in texture, and circinate (= in rings) clusters of pustules occur more frequently in *P. arenariae*, sometimes infections of the two species can look very similar in the field and can even appear together on the same leaf (Fig. 4). A third campion rust, confusingly with the same specific epithet as *P. behenis*, is *Uromyces behenis*. This was not included since it has only been recorded on bladder and sea campions (*Silene vulgaris* and *S. uniflora*), has a different combination of spore stages, and is readily distinguishable from the two species in the survey.

Method

The essential requirement of the 2011 survey was that the spores of every specimen must be checked microscopically. Contributors were asked to send material, ideally of two or more rusted leaves from two plants at each site, and to continue recording throughout the year. The majority of the 60 contributors sent pressed rusted leaves to me, whilst experienced rust recorders checked spores themselves, and a few people sent photomicrographs of the spores. A monthly news sheet reporting progress was sent to all and contributors were urged to continue recording both at the same and different sites. Over the year two-thirds of contributors sent in records on more than one occasion and also new contributors were added. It was only in August that it was appreciated that although red campion was difficult to find in eastern England, rusted white campion (*Silene latifolia*) was present there. Through the news sheet contributors were asked also to record rust on white campion.

Results on red campion

Seasonal development of the two rust species

Red campion is perennial with basal leaves persisting for all or most of the year (Fig. 8).

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There was a preponderance of *P. arenariae* when rust records began to increase early in the plant's growing season (April to June), with *P. behenis* catching up later (Table 1). During the autumn peak fungus recording season there were similar numbers of records of the two species. Overall the ratio of records of *P. arenariae* to *P. behenis* is 1.2 : 1.

Table 1. Number of rust records on red campion in each month during 2011

Months	<i>P. arenariae</i>	<i>P. behenis</i>
Jan	-	-
Feb	-	1
Mar	2	1
Apr	9	3
May	30	9
Jun	56	28
Jul	78	66
Aug	38	54
Sep	57	54
Oct	44	32
Nov	47	46
Dec	21	18
Total	382	312

There was a difference in their patterns of spread, with *P. arenariae* occurring as relatively few individual infections, each soon forming circinate clusters of pustules, whereas *P. behenis* was more 'explosive', and often appeared as many scattered single pustule infections especially later in the year (Figs. 5 & 6). These single pustule infections might later develop into circinate clusters.

Distribution

Although there were few individual collections containing both rust species, comments were received that the other species was found within a short distance. Accordingly the 1 km National Grid square was used as the unit for comparison of the relative distribution of the two species. The presence of each rust species in the 1 km squares containing rusted red campion was counted giving the red (*P. arenariae*) and blue (*P. behenis*) numbers in each of the 100 km lettered squares (those defined by the letters in the OS grid refer-

ences) in Britain (Fig. 7). No records were received from the Channel Isles or Ireland. In the rest of Britain rusted red campion was recorded in 376 1 km squares and in these *P. arenariae* was present in 72% and *P. behenis* in 64%, with both species present in 36%.

Most of the blank lettered squares were in the Scottish highlands and islands. Eight lettered squares had only one of the two rust species recorded, all based on very few (1 or 2) collections. In all the other 100 km lettered squares both rusts were recorded, although the sample size (of 1 km squares) varied greatly, from 1 to 90. In most 100 km lettered squares each rust species occurred in a high proportion (50 to 90%) of the sample. Over most of Britain neither species was predominant in a discernible region. The exception is northern Scotland where, of the 19 sampled 1 km squares in NH, NM and NO, 90% contained *P. arenariae* and only 22% *P. behenis*, suggesting that there was less *P. behenis* up there.

This survey shows that *P. behenis* was widespread and only a little less common than *P. arenariae* in most of Britain in 2011. The next puzzle is what evidence is there about the history of occurrence of *P. behenis*?

Comparison with earlier records

Major sources of earlier records are the database, *Fungus Records Database of Britain and Ireland* (FRDBI), which includes Herb K, the list of herbarium specimens at the Royal Botanic Garden Edinburgh and the database of Welsh rusts compiled by Nigel Stringer (pers. comm.). Combining all these sources, before 1998 there were between 0 and 7 records of *P. behenis* per decade, in comparison with consistently more, between 2 and 162, records per decade of *P. arenariae*.

One difficulty in interpreting earlier records is that records in national herbaria are based on herbarium specimens, which tend to over-emphasize rarities. A difficulty about FRDBI records without herbarium specimens is not knowing the criteria on which each record is based, potentially varying from a distant field sighting to a microscopic check.

Information supporting the view that *P. behenis* was rare before 1998 can be obtained from records on FRDBI made by individuals



Fig.1. *Puccinia arenariae* teliospores (approx 38 x 15 µm).

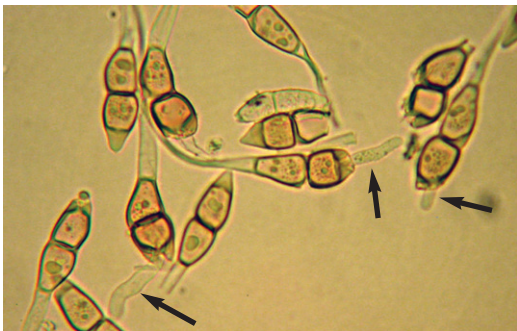


Fig. 2. *Puccinia arenariae* teliospores with some germinating from the apical cell (arrowed).



Fig. 3. *Puccinia behenisi* single-celled urediniospores (approx 24 x 21 µm) and a mature two-celled teliospore (30 x 21 µm).

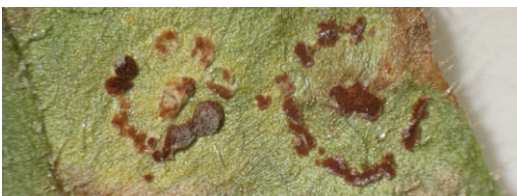


Fig. 4. Circinate clusters of telia of *Puccinia arenariae* (left) and *P. behenisi* (right) on the same leaf of red campion.



Fig. 5. Circinate clusters of telia of *Puccinia arenariae* on red campion, October 2011.

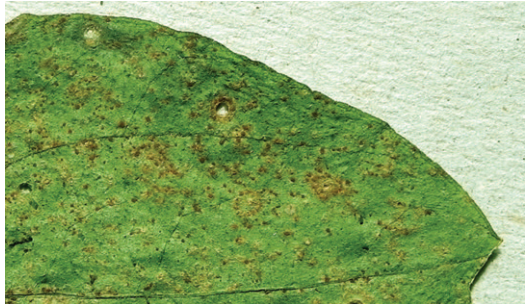


Fig. 6. Many mainly scattered uredinia of *Puccinia behenisi* on red campion, October 2011.

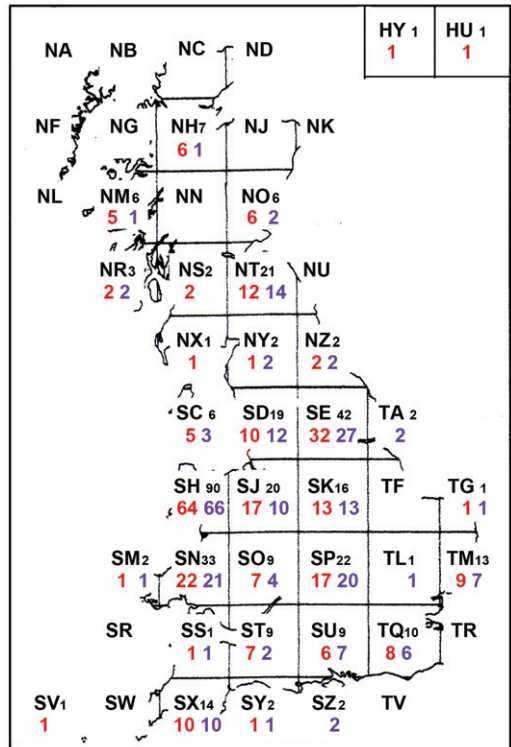


Fig.7. Numbers of 1 km squares reported as containing *Puccinia arenariae* (red numbers at left) and *P. behenisi* (blue numbers at right) in 100 km (lettered) OS squares, with the total number of productive 1 km squares in black.

Figs 1–6 © A.W. Brand.

known to have taken an interest in rust fungi. Although Willis Bramley, the noted Yorkshire mycologist, recorded *P. behenis* on red campion in 1939 all the rest of his 11 records between 1939 and 1972 are of *P. arenariae*. Following Bramley in Yorkshire, Chris Yeates recorded *P. arenariae* 27 times between 1985 and 2002 with only one record of *P. behenis* in 1999. In Warwickshire the Fungus Survey began in 1965 with strict criteria for identification and confirmation of each specimen (Clark, 1980) and before 2002 all 18 Warwickshire records on red campion were of *P. arenariae*, partially confirmed by a check on the six pre-2002 herbarium specimens. In North Lincolnshire Jack Houghton, who took close-up photographs of rust pustules, had found *P. behenis* on white campion in 1987 but all 18 records on red campion between 1982 and 1991 were of *P. arenariae*. At 25 scattered locations Jerry Cooper between 1987 and 2000 recorded only *P. arenariae* on red campion except for 1 record of *P. behenis* in 1998. In Kenneth Payne's specimens and notes (held in Leeds Museums and Galleries Collections) there are 15 records of *P. arenariae* between 1946 and 2005, with his first and only record of *P. behenis* in 2001, confirmed from the herbarium specimens.

Records on FRDBI from 1998 and 1999 signal a greater proportion of *P. behenis* but only in certain areas. At the BMS foray on Arran (NS) in

1998 four localities produced records of both *P. arenariae* and *P. behenis*. In 1999, in addition to Chris Yeates's Yorkshire record, Nick Legon reported several records of both *P. arenariae* and *P. behenis* at four localities in North Somerset (ST)) and Surrey (SU/TQ). However there has been no further recording of these fungi on Arran and only *P. arenariae* has been recorded subsequently in ST, until the 2011 survey.

After 2000 on red campion the detailed and microscopically-confirmed records of rust fungi in Wales, compiled by Nigel Stringer from his own and other observations, can be combined with records from those in England and Scotland (FRDBI and Roy Lemmon, personal comm.) who recorded both *P. arenariae* and *P. behenis* at least once during this period (Table 2).

These point to an increase, at least in these areas, in the proportion of records of *P. behenis* starting in 2003 which has been maintained over subsequent years. Similarly Chris Yeates in Yorkshire (mainly but not exclusively in SE) reported that half of his records of *P. behenis* had been made in the last 4 years (personal comm., 2010). On FRDBI alone over the decade, after allowing for duplicate entries with the same date, location and recorder, the ratio of *P. arenariae* to *P. behenis* remained high, at 7.3 : 1. There is an excess of records of *P. arenariae*.

Table 2. Records made by selected rust recorders of *P. arenariae* and *P. behenis* on red campion between 2000 and 2010

Compiled from Welsh Rust Records (Nigel Stringer, personal comm.), FRDBI records and Roy Lemmon, (personal comm.)

Year	Number of records		ratio records <i>P. arenariae</i> to <i>P. behenis</i>	100 km grid squares containing <i>P. behenis</i>
	<i>P. arenariae</i>	<i>P. behenis</i>		
2000	17	3	5.7 : 1	SM SS SW
2001	15	3	5.0 : 1	HU SN
2002	55	8	6.9 : 1	SH SN SO SP TQ
2003	64	25	2.6 : 1	SH SN SP SS
2004	49	36	1.4 : 1	SH SN SS SX
2005	63	37	1.7 : 1	NT SN SS
2006	18	25	0.7 : 1	NT SK SN SP SS TQ
2007	12	9	1.3 : 1	NT SN SP
2008	31	19	1.6 : 1	SE SK SN
2009	10	5	2.0 : 1	SK SN SO SU
2010	23	20	1.2 : 1	SM SN SP SS SZ

Records on white campion

With little recording on white campion before August there were only 40 records during 2011, giving a *P. arenariae* to *P. behenis* ratio of 0.5 : 1. Samples of rusted white campion were obtained from 22 x 1 km grid squares, and 88% of these contained *P. behenis* in comparison with only 45% containing *P. arenariae*. There was some evidence of a regional difference, with only *P. behenis* recorded in all the sampled more easterly 100 km grid squares in England (Table 3, squares SE and those with T Eastings).

Table 3. Records of *P. arenariae* and *P. behenis* in 100 km OS grid squares on white campion during 2011 (based on between 1 and 3 records per square)

<i>P. arenariae</i> alone	ST SU
Both <i>P. arenariae</i> and <i>P. behenis</i>	NT SK SN SO SP
<i>P. behenis</i> alone	NH SE SJ TG TL TM TQ

The two host species hybridise and one pair of recorders distinguished hybrids (*S. x hampeana*) and showed that both rust species occur on them in NT.

On FRDBI there are only 22 earlier records on white campion, including 14 records of *P. arenariae* and 8 of *P. behenis*, a higher proportion of the latter (1.8 : 1) than on red campion.

Discussion

The maps on the website of the Botanical Society of the British Isles show that red campion occurs commonly and widely in Britain, less so in northern Scotland. White campion is widespread but has a more easterly distribution with fewer records in the west, in Devon, Wales, north-west England and especially Scotland. The two host species hybridise and some pink flowered hybrids may have been included with red campion.

In this 2011 survey, using microscopic characters to distinguish the two rust species, both rusts were widespread on red campion, with *P. behenis* little less common than *P. arenariae*. Regional differences were not detected, although

the sparse information from northern Scotland suggests a preponderance of *P. arenariae* there.

There is good evidence from the records of past and present rust specialists that although *P. arenariae* was consistently widespread, *P. behenis* occurred infrequently on red campion before 1998. The proportion of *P. behenis* increased around the turn of the 21st century and since 2003 has continued at a high level despite yearly fluctuations in the total number of records. During the last decade the continued excess of records of *P. arenariae* on FRDBI cannot be due to this species being more common in the autumn. It could be because of scarcity of *P. behenis* in some regions or possibly this species was sometimes mistaken for the similar-looking *P. arenariae*, as suggested in the Checklist of the *British and Irish Basidiomycota* (Legon & Henrici, 2005).

The few records of both rust species on white campion indicate a similar trend of a greater proportion of *P. behenis* in 2011 than in previous records, but with an overall bias towards *P. behenis*.

This leads to the ultimate puzzle: why has *P. behenis* increased? What change occurred around the turn of the century that has persisted over years and regions? This is inevitably speculation and possibilities include changes in the abundance of other host plants, man-made environmental changes in habitats and climate change.

P. arenariae occurs on other host species in the *Caryophyllaceae* (Henderson, 2000) and infection studies by early mycologists indicate that cross infection can occur. *P. behenis* also occurs on sea campion (*Silene uniflora*) and bladder campion (*S. vulgaris*) but there are few records on FRDBI.

Habitats were not specifically asked for in this survey. The majority of my records of both species (square SP) were from road and pathsides and showed a preponderance of *P. behenis*. The best specimens that were sent in of *P. arenariae* alone were from within woodland, especially at infrequently visited locations. White campion is characteristically a plant of roadside verges. The basidiospores of *P. arenariae* are discharged actively with a drop of liquid as in *Hymenomyces* (Buller, 1924). The dry wind-borne urediniospores of *P. behenis* could be dispersed by the greater air movement along the sides of roads and paths.

P. behenis is now widespread. In comparison with larger fungi the rust fungi are poorly recorded. These survey records will be placed on FRDBI and will provide a benchmark for comparison with future records.

Acknowledgements

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Stop Press!

During 2012 records have been received from an additional 100km grid square: both *P. arenariae* and *P. behenis* in SW (West Cornwall, Pauline Penna).

References and websites

Books

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Internet Links

- Botanical Society of the British Isles (BSBI) Maps Scheme. <http://www.bsbimaps.org.uk>
- Fungal Records Database of Britain and Ireland (FRDBI, managed by the British Mycological Society) <http://www.fieldmycology.net/FRDBI/FRDBI.asp>
- Mycologia Scotica. <https://sites.google.com/site/scottishfungi/mycologia-scotica>



Fig. 8. Red campion, *Silene dioica* showing its bifurcated petals. in roadside verge on Crossway Rattle Hill, near How Caple, Herefordshire, England. May 2010. Photograph © Tony Bailey.